PROC. ENTOMOL. SOC. WASH.
95(1), 1993, pp. 113–125

THE FIRST *HOLCOPASITES* FROM WESTERN CALIFORNIA, *H. RUTHAE* N. SP., AND *H. LINSLEYI*, A NEW SPECIES FROM SOUTHWESTERN ARIZONA (HYMENOPTERA, NOMADINAE)

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Abstract.—Described are ***Holcopasites ruthae*** n. sp. from coastal sage scrub, the first species known from western California, and ***H. linsleyi*** n. sp. from southwestern Arizona, with notes on separation of both from similar species. Setose eyes are an attribute of species of *Holcopasites*, and at least the male of *Schmiedeknechtia gussakovskyi* Popov. Warncke's synonymization of the Nearctic *Holcopasites* with the Palearctic *Schmiedeknechtia* is briefly discussed, and for the present rejected.

Key Words: *Holcopasites*, new species, habitat, *Schmiedeknechtia*, synonymy

From the end of April through May of 1991, I found a striking new species of *Holcopasites* in moderate numbers on campus land of the University of California at Riverside. That occurrence is astonishing, for the general area had been intensively collected throughout the year, and nearly every year for 40 or more, by that paragon of collectors and authority on wild bees, P. N. Timberlake. Neither he, nor any other of the noted collectors of California bees have been fortunate enough to come upon this species, nor had I previously over a period of 23 years.

But two species of *Holcopasites* had earlier been found in California, in marked contrast to the twelve known from Arizona: a single specimen of *H. stevensi* Crawford, of unknown provenance, very old and labelled simply "Cal.," and four specimens of *H. bohartorum* Hurd and Linsley from southeastern California: 18 miles west of Blythe (Wiley's Well).[1] The new species is the first record of a member of the genus *Holcopasites* from western California.

The exact type locality, where all but two specimens of the new species were captured, is currently undeveloped. It is a small elevation of flatland, or "mesa," with a gentle downslope to the west (altitude 340 m, slope ca. 0.1°, where the bee was found). It remains a shrinking enclave of coastal sage scrub, from time to time reduced by university usages. It is now surrounded by developed areas, none more than 0.3 km distance: to the north and below a huge (674 vehicles), paved parking lot on level land formerly covered with scrub continuous with that on the mesa; adjacent and to the west, experimental groves; to the south, more agricultural land and the U.C.R. Botanic Garden; and to the west its downslope ending at a paved road and extension of the parking lot (64 vehicles) to the north. Amid the remaining scrub are scattered clumps of *Encelia farinosa* Gray & Torr. at which the *Holcopasites* were exclusively taken.

Nearly all of the bees were captured on the flat land of the mesa, within an area of less than 0.2 hectare. Apparently the *Hol-*

[1] Of the four specimens, one not earlier recorded was kindly given me by its collector, Dr. Eric M. Fisher of the California Department of Agriculture (date of capture: 8-IV-1972).

copasites shunned the downslope, even though flowering *Encelia* were equally abundant to each side of a dirt service road cut through the sloping land. Almost certainly that preference owed to the fact that the probable hosts of the bee are panurgine bees that nest on bare, level patches of ground, as is the case for known host bees of other species of *Holcopasites*. On the flatland of the mesa both *Holcopasites*' probable host, and the preferred flower of each was present.

An absence of suitable level nesting areas on the adjoining terrain, including the Botanic Garden, accounts for the scarcity of *Holcopasites* despite suitable stands of *Encelia*. Regrettably, not knowing the life span of the adult *Holcopasites*, I was too late in the season to find areas in which the likely host, *Calliopsis pugionis* Cockerell, was nesting.

Methods

The distance from the costal sclerite to the fenestra between the pre- and pterostigma is a useful relative measure of length. It is ordinarily easily made, with good precision, and makes it possible to match related bees of comparable body sizes, regardless of flexion of head and metasoma and differing degrees of distention or contraction of the latter.

Statistical summaries of measured attributes and ratios include the median value only when mean and median differ. Because estimates of the coefficient of variability (V) from small samples tend to be too low, Haldane's (1955) $V^* = \left(1 + \frac{1}{4n}\right) \cdot V$ is given as a "nearly unbiased estimate." If no n is stated in a summary, the sample size is 16 for females, or 30 for males, namely all in the collection of the given sex.

Where certainty concerning the presence and distribution of very small ocular setae, or a very small, low labral papilla (= vestigial tubercle?) was required, a Leitz Ultropak lens with an annular condenser was used at a magnification of ca. 110×. Nevertheless, with attention to lighting, even the smallest ocular setae (but not their distribution) and labral papillae are detectable with a stereoscopic binocular microscope at magnifications of 50×.

Description.—Items preceded by an asterisk (*) are chief among those by which the first new species regularly or ordinarily differs from the described attributes of *H. stevensi* observed by Hurd and Linsley (1972) in a large sample of 162 females, 30 males, and the 5 females and 5 males at hand. Characterizations within quotation marks are from Hurd's and Linsley's description of *H. stevensi*.

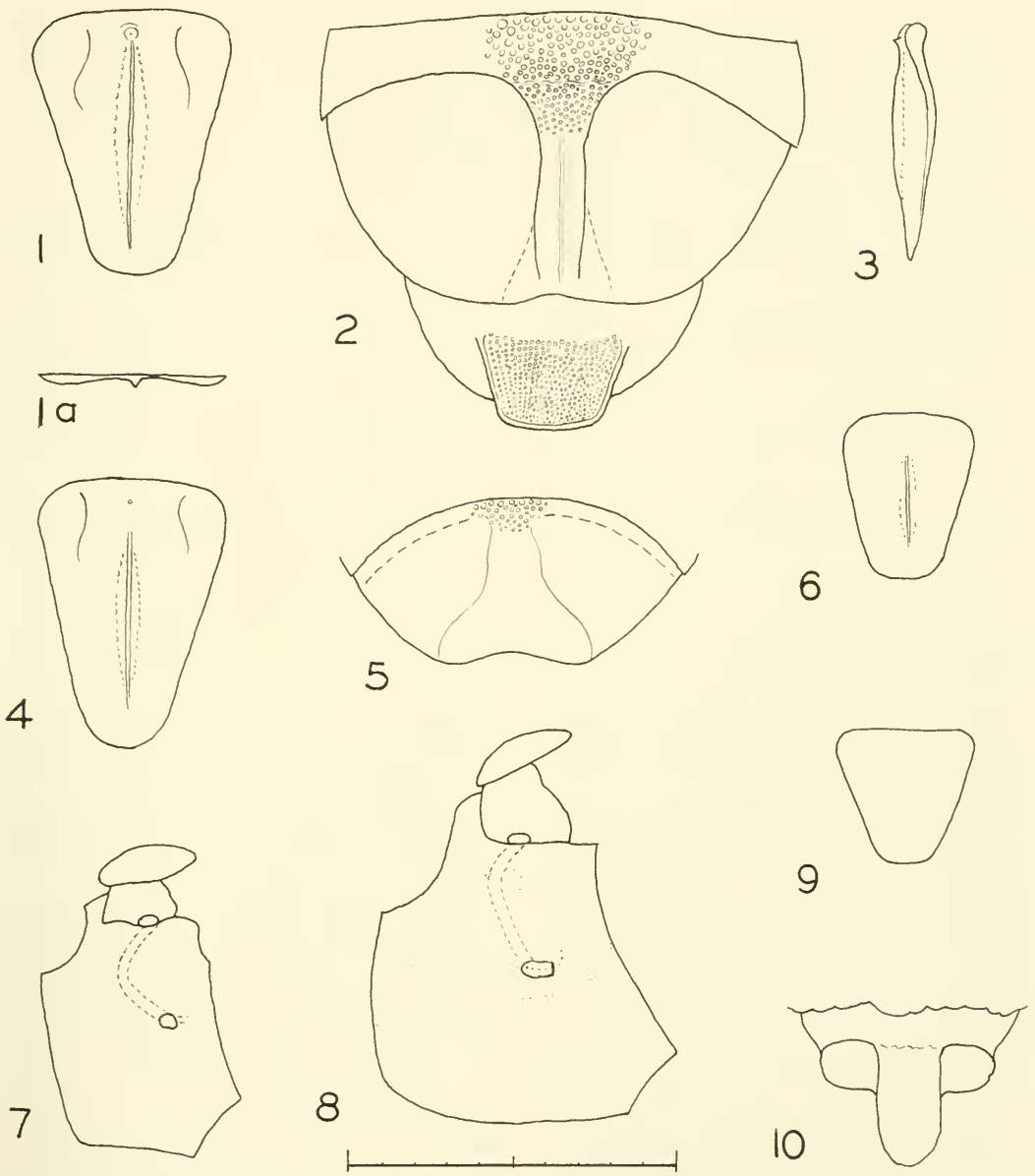
Apart from the terminal metasomal segments, and a tendency for dark areas of the metasoma to be darker in males, males and females of *H. ruthae* are externally similar. Identically numbered attributes (in parentheses) in the descriptions of both sexes denote those by which many or all males differ from females to a significant degree, easing cross-reference and constituting a partial list of secondary sexual attributes that are in addition to differences in the terminal metasomal segments and tarsal claws (Linsley and Michener, 1939).

Holcopasites ruthae Cooper, New Species

(Figs. 1, 1a, 2, 3, 8, 9, 10)

Recognition.—Both sexes of *H. ruthae*, a banded species, are set apart from other described species by a small, median tubercle at the base of the labrum from which a strong, longitudinal labral carina directly arises; tubercle about as high as greatest height of carina (Figs. 1, 1a, 3). It also differs from *H. stevensi* Crawford, the only species with which it is likely to be confused, by its vernal flight period; *H. stevensi* flies from July to September, temporally isolated from *H. ruthae*.

Female (16 specimens).—Length, observed range = 5.1–6.6 mm, $\bar{m}$ = 5.8 mm, median = 5.7 mm, V* = 8.2; of forewing



Figs. 1–10. Scale = 1.0 mm. All figures drawn from camera lucida outlines, hence somewhat asymmetric and semidiagrammatic. Figs. 1–3, 8, 10, *Holcopasites ruthae* n. sp.: 1, Labrum, anterior surface with medial, basal tubercle and carina; 1a, transverse section of labrum at level of basal tubercle. 2, Terga-5 and -6 of female—gradulus and "pseudopygidium" (= medial ridge) of t-5; pygidum of t-6. 3, Labrum, left lateral aspect. 8, Mesepisternum, furrow from subalar pit to scrobe, and outline (dotted) of inner margin of open ring of white plumose setae. 10, Tergum-7 of male, gradulus, posterior ventral margin, and pygidium. Fig. 4, *H. stevensi* Crawford: Labrum, anterior surface with small papilla (not formed in all specimens) and medial carina. Figs. 5, 6, *H. linsleyi* n. sp.: 5, Tergum-5 of female, showing gradulus and large pseudopygidium. 6, Labrum, anterior surface with short, median carina. Figs. 7, 9, *Schmiedeknechtia gussakovskyi* Popov: 7, Mesepisternum: contrast proportions with that of *Holcopasites* (Fig. 8). 9, Short carinaless labrum, anterior aspect.

from apex of costal sclerite to fenestra between pre- and pterostigma: obs. r. = 1.8–2.1 mm, $\bar{m}$ = 1.9 mm, V* = 5.6.

Integumentary coloration.—Head and mesosoma black to very dark piceous; antennae black, dark brownish toward apex; mandibles exernally banded, tips dark to reddish brown, medially reddish, basally black and piceous, inner surface reddish; anterior smooth margin of clypeus black to dark brown; (1) labrum black, piceous to reddish brown laterally and apically; tegulae brown, margin translucent, a transverse clear band divides discal brown area; forewing iridescent, lightly infumate, slightly darker apically, *(2) a sooty area within apex of marginal cell, darker from apex of cell along wing margin, ending before wing tip; hindwing membrane similar but less infumate; legs black to dark piceous, tibia-3 deep reddish brown in some; tibial spurs: malar spine brown, spurs of tibiae-2, -3 dark brown, reddish brown in some; *metasoma: red, terga-2 to -5 increasingly darkened medially from brownish red or brown to piceous, black in some; tergum-6 testaceous.

White markings.—Conspicuous white, appressed, squamiform, plumose setae decorate the contrasting integuments with spots, bands, and scattered arrays as follows:

On head: Surrounding antennal bases and over the median facial carina to (or nearly to) median ocellus; 1–5 setae within ocellar triangle; (3) a scattering or patch on upper genae, usually less in length than maximum width of eye; clypeus (except at fronto-clypeal suture) without squamiform setae.

On mesosoma: A band on upper margin of pronotum and along margins of pronotal lobes; a narrow, posteriorly convergent patch on anterior third (or less) of mesoscutum divided lengthwise by medial scutal furrow; a lateral edging of mesoscutum reaching tegulae, a loose patch behind tegulae; (4) a band forming a ring on upper mesepisternum, covering subalar pit and lower half (or more) of scrobe, anterior to scrobe the ring is generally open (Fig. 8), or weakly closed by scattered squamiform setae; patch or scattering along axillae, scutal-scutellar suture, and scutellar rear margin; a small scattering above mesocoxa; dense coverings on lateral wings and projecting lateral angles of metanotum; scattering of *small* squamiform setae along upper lateral margin of propodeal triangle, below hindwing and above spiracle; scatterings ventrally along margins and distally on both meso- and metasterna.

On legs: On coxae anteriorly above, successively larger on meso- and metacoxae, half to one-third of ventral margins of femora-2, -3; (5) a loose band along dorsal margin of tibia-3.

On metasoma: A small postero-lateral spot and broad patch on anterior outer thirds of tergum-1 on each side, lapping over margin onto anterior face; terga-2, -3, -4 with small elongate postero-lateral spot and narrow anterior band on each side of middle; (6) none to one or more small, disconnected patches in subapical depression of posterior margin of tergum-4; tergum-5 without squamiform setae; (7) slender, more or less squamiform white setae on sternum-1, forming transverse basal bands on sterna-2 to -5; bands of short, inconspicuous, white hair along apical margins of sterna-2 to -4.

Other vestiture.—Clypeus with slender, yellowish plumose hairs sparsely distributed along anterior margin; *labrum with narrow, subbasal transverse fringe of long (greater than an ocellar diameter), nearly erect, slender, yellowish plumose hairs. Wing membranes with minute hairs, more dense beyond apical venation; ridge along ventrolateral face of hind tibia with row of long setae, tips bent ventrally; median ridge of tergum-5 widened anteriorly and posteriorly, bare above, fine silvery hairs over posterior two-thirds; tergum-6 with fine, lengthwise, subparallel silvery hairs on pygidium.

Structural features.—*Of head:* Flattened ventrally and posteriorly; width to length, observed range = 1.13–1.19, $\bar{m}$ = 1.16, V* = 1.5; head width to mesonotal width, obs.

r. = 1.11–1.21, $\overline{m}$ = 1.18, V* = 2.4; (8) clypeal width to length, obs. r. = 2.78–3.06, $\overline{m}$ = 2.92, med = 2.94, V* = 2.8 (N.B., fronto-clypeal suture overlain by squamiform setae); (9) labral length to width, obs. r. = 1.31–1.46, $\overline{m}$ = 1.38, med = 1.40, V* = 3.3; *eyes with short setae over entire surface except above the darkened rim; setae 12–15 μm long, visible at 50×; face coarsely punctate, puncta largest between upper margin of eye and ocelli, interspaces shining; *antennae with flagellar article-1 subequal to articles-(2 + 3), obs. r. = 0.92–1.08, $\overline{m}$ = 1.01, V* = 5.6, n = 15; distance from lateral to anterior ocelli subequal to distance between lateral ocelli from 0.23 to 0.31 mm ($\overline{m}$ ~ 0.26 mm); width of median ocellus; *(10) least ocellorbital distance to lateral interocellar distance from 1.12 to 1.31 ($\overline{m}$ = 1.19, V* = 3.8); posterior articulation of mandible slightly posterior to midpoint of lower margin of eye; (11) acetabular carina low at base; (12) clypeus with lateral extremities rounded, lateral carina (above clypeogenal suture) weak; *labrum with small, basal tubercle (use 50×), little more than own basal diameter from anterior margin of labrum, from which a well-defined carina (lower immediately behind tubercle) extends length of labrum, or nearly so, height of tubercle about same as greatest height of carina (Figs. 1, 1a, 3); *labrum punctate, densest basally (no basal, mesal, impunctate strip); punctation extending onto sides of carina, punctal size decreases laterally and distally, interspaces polished (at 50×); postgena uniformly, closely, coarsely punctate to hypostomal carina, interspaces less wide than punctal diameter; mouth parts short, reaching very slightly beyond proboscidial fossa.

Of mesosoma: Mesoscutum closely, coarsely punctate; tegulae with a strong, concentric microsculpture (at 50×), few discal puncta, mesepisternal puncta not "nearly rugosely punctate," interspaces ca. one-third of punctal diameters; a weakly impressed sulcus on mesepisternum, arising below subalar lobe, near subalar pit, ending in scrobe (Fig. 8); scutellum simple, posterior margin subtruncate, at most very slightly indented postero-medially; ratio internal length of marginal cell to distance from its apex to wing tip: obs. r. = 1.08–1.16, $\overline{m}$ = 1.13, V* = 6.0, n = 13; metanotum angularly produced to each side; a well-defined triangular region on upper metapostnotum of strong microsculpture, medially closed meshes, laterally and posteriorly appearing as though tracts of fine carinulae, triangular area about a third as long as wide.

Of appendages: Second submarginal cell three-fourths or more length of first along posterior sides; calcar of mid-tibia ca. one-half length of basitarsus; anterior, dorsal apical ends of mid and hind basitarsi projecting, spinelike.

Of metasoma: Tergum-5 with bare, coarsely punctate, piceous or black raised area at base of tergum interrupting gradulus medially, with a low lengthwise mesal ridge, widened below, forming a weak pseudopygideal area (Fig. 2); apex of tergum nearly truncate, slightly insinuate; pygidial plate of tergum-6 with sides slightly convergent apically, rounded apico-laterally, strongly punctate, puncta strongest proximally (Fig. 2); sternum-5 shallowly impressed medially in apical half, apex subtruncate, projecting beyond tergum-5; lateral lobes of sternum-6 nearly 0.6× as long as distance between them; each lobe at apex with 4 to 6 stout, curved, blunt setae below (m = 5.06, V* = 10.5, n = 16; no cases in which both lobes had 4 or 6 such setae), 10–12 additional lesser setae apically, slender hairs externo-laterally and ventrally on lobes, very long hairs, especially on sides, in the horizontal plane within (above a close fringe of very short hairs along inner rim of sternum), tips of those in basal half nearly meeting medially.

Male (30 specimens): Similar in coloration and habitus to female. Length, observed range = 5.1–6.6 mm, $\overline{m}$ = 5.6 mm, V* = 5.8; of forewing from apex of costal

sclerite to fenestra between pre- and pterostigma, obs. r. = 1.7–2.3 mm, $\overline{m}$ = 1.9 mm, med = 1.8 mm, V* = 6.7; for all but the last of the following, a random selection of measured individuals: head width to length, obs. r. = 1.12–1.19, $\overline{m}$ = 1.15, V* = 1.4, n = 16; head width to mesonotal width, obs. r. = 1.15–1.28, $\overline{m}$ = 1.21, V* = 2.2, n = 16; (8) clypeal width to length, obs. r. = 2.45–3.00, $\overline{m}$ = 2.79, V* = 4.8, n = 16; (9) labral length to width, obs. r. = 1.27–1.40, $\overline{m}$ = 1.34, med = 1.32, V* = 3.6, n = 16; length flagellar-1 to flagellar-(2 + 3), obs. r. = 0.91–1.11, $\overline{m}$ = 1.02, med = 1.00, V* = 7.3, n = 15; ratio length of marginal cell to distance from apex to wing tip: obs. r. = 1.06–1.28, $\overline{m}$ = 1.12, V* = 6.0, med = 1.11, n = 25; (10) least ocellorbital distance to inter-lateral ocellar distance, obs. r. = 1.16–1.40, $\overline{m}$ = 1.25, V* = 5.6, n = 30.

Secondary sexual differences, including (8), (9) and (10) above: (1) in 19 specimens labrum wholly black; (2) spot at apex of forewing marginal cell paler, smaller; (3) white patch on upper genae broader, generally longer than maximum width of eye; (4) white ring on the mesepisternum generally closed ventrally; (5) white, dorsal longitudinal band of hind tibia strong; (6) metasomal tergite-4 has no apical white band, a white spot at each postero-lateral angle; tergum-5 has a strong basal white band on each side, and a nearly complete white band in subapical sulcus; tergum-6 has a nearly complete apical white band, anterior to which a weak subapical bisinuation, producing a distinct median lobe in some, margin more or less crenulated; from above, tergum-7 has rounded postero-lateral angles, posterior ventral margin nearly at right angles to pygidial plate axis; pygidial plate parallel-sided (Fig. 10), *length to basal width, observed range = 1.64–2.00, $\overline{m}$ = 1.88, med = 1.89, V* = 7.4, n = 18; maximum width between lateral lobes of tergum-6 to width of pygidial lobe, obs. r. = 2.36–3.06, $\overline{m}$ = 2.72, V* = 7.6, n = 29; pygidium coarsely punctate, margins slightly reflexed; (7) setal and hair bands on sterna as in female, but much stronger; sternum-5 with both bands, apical band weak, often incomplete medially; (11) acetabular carina of mandible raised to a broad, triangular "tooth" at base, apex of triangle translucent amber; (12) clypeus with lateral extremities strongly angulate, lateral carina very strong.

Etymology.—The species name *ruthae* is in grateful recognition of my biologist wife, Dr. Ruth S. Cooper, who has been my constant field companion and scientific helpmate for more than half a century.

Holotype: Female; California, Riverside County, Riverside (University of California Campus), from flowers of *Encelia farinosa,* 18 V 1991; allotype: same locality and flower, but 9 V 1991. Both have been deposited in the U.S. National Museum of Natural History.

Paratypes: All from same general locality and year as holotype and allotype. Dates of capture: females—3 (4 V), 1 (8 V), 1 (9 V), 2 (11 V), 2 (12 V), 4 (13 V), 1 (15 V), 1 (17 V); males—1 (29 IV), 2 (30 IV), 6 (4 V), 4 (8 V), 3 (9 V), 1 (11 V), 3 (12 V), 3 (13 V), 1 (15 V), 2 (18 V), 1 (20 V); the following from *Encelia palmeri* Vasey & Rose in adjoining U.C.R. Botanic Garden, both males: namely 1 (collected by David Hawks, 4 V), 1 (15 V).[2] The last individual seen was on June 1.

Distribution: Paratypes will be deposited in the collections of the American Museum of Natural History, the British Museum (N.H.), the California Academy of Sciences; The University of California (at Berkeley, Davis, and Riverside), the Snow Museum of the University of Kansas, the Systematics Laboratory of the California Department of Agriculture, and the Bee Biology and Systematics Laboratory, Utah State University.

Possible host: Calliopsis pugionis Cockerell was common at the same flowers of

[2] The labels on specimens have the months indicated by a *single letter*; thus A or a = January, B or b = February, etc.; thus 29 d 91 or 91 D 29 = 29 IV 91.

Encelia before, during, and briefly after visits to them by *H. ruthae* had ended.

Taxonomic.—It should be noted that my sample of 46 specimens of this new species differs from most other large series of *Holcopasites* species, for all were collected at one small site in the same year. They may therefore display less variation in dimensions, coloration and vestiture than would a series of corresponding type from different years and from a variety of localities. For reasons discussed in the closing commentary, unless a specimen's eyes are strongly setose, all identifications should commence with Hurd's and Linsley's key (1972, p. 11).

Male *H. ruthae* reach couplet 5 of Hurd's and Linsley's (1972) key to the banded species. They differ (among other ways) from *H. illinoiensis* Robertson of that couplet by their apical metasomal terga which are not "chiefly or entirely blackish." Unlike the alternative, *H. stevensi,* the apical metasomal terga are not "at most vaguely clouded with blackish"; in *H. ruthae* markings are definite, clearly darker, often greatly so, than adjoining integument.

Female *H. ruthae* first run into ambiguity in couplet 10, for in *H. ruthae,* the first flagellar segment is subequal to, "or slightly longer than . . . combined length [of] succeeding two segments" as in *H. illinoiensis*; but from the latter it differs by having the ventral surface of head (the hypostomal area) closely punctate, not "sparingly punctate." Nor does *H. ruthae* fit either species separated by couplet 11. From *H. eamia* (Cockerell) it differs by having a strongly carinate labrum (I find no labral carina in *H. eamia,* nor has one been described by others), and by lacking "a subtriangular patch of white pubescence on either side of the middle" of metasomal tergum-4. Differences from the other member of the couplet, *H. stevensi,* are given below.

Most *H. stevensi,* perhaps all but a minority, can be separated from *H. ruthae* by their paler metasomata, and generally by an absence in both sexes of successively darker, brown to blackish, medial integumentary areas from tergum-2 to the last, and a somewhat greater squamiform setation of most of the closely corresponding white markings of head and body.

Unlike the labrum of *H. ruthae,* most *H. stevensi* have a mesally elongated, polished strip basally (upon which a tiny papilla may be found near its base in many—see Fig. 4); the median carina generally arises from the distal end of a polished mesal strip; basal brush of labral plumose hairs (if not abraded) not a simple transverse, near-linear array, but relatively wide, at mid-width almost reaching dorsal margins of closed mandibles. In *H. stevensi* the ocular setae are very much sparser; "first flagellar segment is shorter than the two succeeding segments"—in *H. ruthae* that ratio is female (0.92–1.08×, n = 16), male (0.91–1.11×, n = 30). *H. stevensi* has the "interocellar and ocellocular distances about equal"; in *H. ruthae,* the ratios of the distance between posterior ocelli to the ocellocular distance are: female (1.12–1.31×), male (1.25–1.40×). Spot on forewing at the apex of the marginal cell in female *H. stevensi* is very pale and short, still weaker in the male; the spot both larger and darker in both sexes of *H. ruthae.* Female *H. ruthae* have the two inner patches of the distal white band of tergum-4 short and poorly differentiated or, more often, lacking entirely; in *H. stevensi* that distal white band is well-formed, with the two inner patches strongly marked and much elongated (see fig. 13, Hurd and Linsley 1972). The male pygidial plate of *H. stevensi* is said to be "more than twice as long as maximum basal width." In *H. ruthae* the pygidial length *and* basal width could be measured in 18 males only, for in the remainder the base of the pygidial plate is covered by the apex of tergum-5; observed range in length to width is 1.64–2.00×. The above differences, and different seasonal flight times of the two bees, justify recognition of two entities by individual specific names.

Holcopasites linsleyi Cooper, New Species
(Figs. 5, 6)

Recognition.—The single female specimen is a member of the banded-species group. It differs strikingly from all described female *Holcopasites* by its predominantly ferrugineous integument and well-formed trapezoidal pseudopygidium, widest apically, of metasomal tergum-5.

Female.—Length 3.3 mm; of forewing from apex of costal sclerite to fenestra between pre- and pterostigma 0.9 mm.

Integumentary coloration.—Overall ferrugineous, except as follows: reddish-brown on upper frons, merging with a poorly defined, conspicuously darker, brown band from sides of ocellar triangle to upper frontal orbits; antennae brown above, pale below; mandibular tips dark brown to brown; approximately lateral thirds of mesonotum reddish-brown to brown; scutellum predominantly dark brown; tegulae brown, outer margins narrowly transparent, a broader transverse transparent band divides pigmented disc; wings iridescent, membrane grayish, veins brown, darker along leading edge and apically; anterior surfaces of femora-1, -2, paler, dark brown elsewhere; femur-3 pale anteriorly in basal two-thirds, posteriorly in basal half, dark brown elsewhere; tibiae dark brown; shaft and spine of malus yellow, tibial spurs brown; tarsi dark reddish-brown; metasomal tergum-3 with a transverse, dark brown spot medially; tergum-4 with a large, blackish-brown, medial, transverse area from near base to apex, narrowing laterally, covering about half of disc. Tergum-5 with a dull, grayish-brown, well-formed pseudopygidium, widest apically; broad, subbasal dark brown band reaching lateral margin, enclosing a dully ferrugineous spot each side of pseudopygidium; sternum-5, except for basal and antero-lateral margins, reddish-brown.

White markings (by appressed, squamiform setae).—*On head:* Above and onto upper clypeus, surrounding antennal sockets and along median facial carina nearly to median ocellus; a band across vertex, broadening laterally onto upper halves of genae.

On mesosoma: Along upper margin of pronotum onto base and rear of pronotal lobes; a posteriorly narrowing, elongate patch on basal half of mesoscutum divided lengthwise by median scutal furrow; lateral edging from antero-lateral margin of mesoscutum to transverse scutel-scutellar suture; dense patch covering each axilla, posterior margin of scutellum (within a shallow subapical furrow), and projecting lateral angles of the metanotum, between which transverse median portion is bare; narrow strip above propodeal spiracle, attenuating along upper lateral angles of triangle; dense, very large, roughly pentagonal patch over upper two-thirds of mesepisternum, posterior extension of which reaches nearly to mesocoxal margin; sparse, squamiform hairs along uninflected anterior margin of mesepisternum connecting large pentagonal patch with that to each side of the median mesepisternal sulcus ventrally and along meso-metasternal sutures, within and along borders and distal process of the metasternum; to each side of the main tracts of large squamiform setae on mesepisternum successively shorter, more slender, less white hairs.

On legs: On coxae a weak scattering laterally; two-thirds to three-fourths of ventral margins of femora-2, -3; a band along dorsal surface of tibia-3.

On metasoma: Tergum-1 anteriorly with a band on each lateral third, concavity with slender hairs, thin scattering of squamiform setae (laterally only) along distal margin; both terga-2, -3 with long bands basally, interrupted medially, on each side an elongate patch disto-laterally, broadest laterally; tergum-4 with elongated basal band interrupted medially, connected with uninterrupted apical band by scattered setae laterally and to each side of the bare, medial black spot, enclosing on each side a small

bare spot of ferrugineous cuticle; tergum-5 has a small scattering of squamiform setae basally on each side; sternum-1 has a triangular patch medially; sternum-2 has an apico-marginal row; sternum-3 has a sparse basal band of small squamiform setae connecting medially with a distal wide band that narrows laterally; sternum-4 appears rubbed, evidently had a distal band similar to that of sternum-3; sternum-5 without squamiform setae.

Other vestiture: clypeal surface with sparse, slender, scantly plumose hairs, largest medially, progressively shorter laterally and along orbits; labrum with sparse, longer hairs on basal third. Wing membrane with minute hairs, more closely spaced beyond apical venation. Pseudopygidium of tergum-5 with exceptionally short, decumbent, silvery hairs.

Structural features.—*Of head:* Globose, very wide, 1.4× wider than long, 1.2× wider than mesonotum; clypeus 4× wider than long; labrum about 1.2× longer than wide (Fig. 6); lateral carina above clypeogenal suture strong; mouthparts short, extending only slightly beyond proboscidial fossa; setae of eyes sparsely distributed over entire surface, setae somewhat longer than ommatidial diameter; face closely punctate, more coarsely on upper frons, narrow interspaces shining; antenna: flagellar segment-1 ca. 0.8 length of flagellar-(2 + 3); more distal flagellar segments somewhat longer than broad, but antennae not unusually long for *Holcopasites* species; distance anterior ocellus to lateral ocellus subequal to an ocellar diameter; distance between posterior ocelli nearly 2× transverse width of anterior ocellus (which is wider than long); distance between posterior ocelli to ocellorbital distance about equal; eyes bulging, posterior articulation of mandible behind midpoint of lower margin of eye; labrum punctate, puncta weakly impressed, largest in basal third, diminishing laterally and distally, without a basal tubercle, with a low, sharp carina from near base to apical fourth (Fig. 6); hypostomal area uniformly, closely, coarsely punctate to hypostomal carina, interspaces narrow, shining.

Of mesosoma: Mesoscutum closely, coarsely punctate; tegulae polished (at 50×), with few, scattered discal puncta; exposed mesepisternal puncta coarse, close set; mesepisternal sulcus ending in scrobe (visible when covering squamiform setae moistened with benzene); scutellum entire, posterior margin weakly, outwardly curved; ratio of length of marginal cell to distance from its apex to wingtip: 0.93; metanotum angularly produced laterally; propodeal triangle on upper metapostnotum with narrow (length ca. 0.2× width), distally slightly curved basal area of microsculpture.

Of appendages: Second submarginal cell of forewing two-thirds length of first along posterior side; calcar of mid-tibia ca. half basitarsal length; hind trochanter with disto-ventral margin spine-like in silhouette.

Of metasoma: Tergum-5 with coarsely punctate piceous raised area interrupting gradulus medially, apex with well-formed, nearly isosceles trapezoidal pseudopygidium, ca. 4.5× wider apically than basally (Fig. 5), densely, minutely punctate, surface dull, very shallowly emarginate posteriorly; pygidial plate of tergum-6: not exposed; sternum-5 medially, longitudinally impressed on apical 0.7; lateral lobes of sternum-6 short, little more than one-third distance between their apices, with three stout, curved, blunt setae apically below, 8–9 lesser setae apically, hairs along inner margins of lobes with tips widely separated along distal half of apical emargination.

Etymology.—*H. linsleyi* is dedicated to E. Gorton Linsley, eminent field naturalist and systematist, whose wide-ranging studies of insects over many years, importantly including *Holcopasites* and other small nomadine bees, and warm friendship have been of such help and pleasure to his colleagues.

Holotype.—Female, Arizona, Yuma County, 2.5 miles east of Aztec, 15 VIII 64, E. I. Schlinger; from the Timberlake Col-

lection at the University of California, Riverside, labelled "*Holcopasites* sp. female, det. Timb." It will be placed in the collections of the California Academy of Sciences in which all recovered types of the Timberlake Collection have been placed.

Comparisons.—There are four other described species of *Holcopasites* of which some females are as small, or smaller, than 3.5 mm. None have either a predominantly ferrugineous integument nor a well-formed pseudopygidium, there being only a low, median, longitudinal ridge on tergum-5. All have significant morphological differences from *H. linsleyi.*

H. pulchellus (Cresson) has the postgena between the hypostomal carina and lower margin of eye polished, with widely spaced, irregularly distributed puncta, as well as a medially cleft, prominently bilobed scutellum. *H. tegularis* Hurd and Linsley lacks a medial labral carina; second submarginal cell of forewing is "much shorter than one-half as long as first submarginal . . . when measured along posterior side." Additionally, both are members of the *spotted* species group.

Of the two small species belonging to the *banded* species group, of which *H. linsleyi* is a member, female *H. cazieri* Hurd and Linsley has the postgena sparsely punctate, polished and shining adjacent to hypostemal carina, and the apex of metasomal sternum-5 deeply emarginate medially.

At first glance, *H. illinoiensis minimus* (Linsley) appears strikingly similar to *H. linsleyi* (apart from coloration). However, like *H. pulchellus* and *H. cazieri, H. i. minimus* has the hypostomal area polished and sparsely punctate; also, flagellar article-1 about equal to flagellar-(2 + 3).

Comment

H. ruthae, H. linsleyi, and *H. stevensi* of the banded species group are not alone in having setose eyes; that is so for *H. cazieri* Hurd and Linsley, *H. eamia, H. illinoiensis* s. str. and *H. illinoiensis minimus* (Linsley). *H. bohartorum, H. calliopsidis* (Linsley), *H. heliopsis* (Robertson) and *H. pulchellus* (Cresson) of the spotted species group also have setose eyes.

In all of the above the setae are of uniform length and, though scattered, occur more or less regularly over the surface of the eye. In *H. ruthae* there is no significant difference in setal lengths of male and female; the setae are very slender and somewhat longer than an ommatidial diameter. Setae of some other species seem to differ in length, and certainly do differ in density over the surface of the eye. *H. eamia,* e.g. has exceedingly widely spaced setae, the sparsest set of ocular setae among all those examined.

In view of the above, it is likely that all *Holcopasites* have setate eyes. Nevertheless *Trichopasites* (Linsley 1942) remains a useful group, for its members stand apart by possession of very long, coarse setae which densely clothe their eyes. Those of *H.* (*Trichopasites*) *insoletus* (Linsley) are appreciably longer than twice the length of the longest setae found among *H.* (*Holcopasites*) species, and appear to be more than three times as wide. The setae of *H.* (*T.*) *arizonicus* (Linsley) are distinctly shorter and narrower than those of *H.* (*T.*) *insoletus.* Nevertheless, they are of such dimensions that none among the spotted and banded species can plausibly be considered to be transitional. Discontinuities in setal dimensions and density over the eyes are vastly different.

I examined a male of *Schmiedeknechtia gussakovskyi* Popov. Its eyes are also setose, but the setae are both shorter (<ommatidial diameters) and much more sparsely distributed than any among the 13 species of *Holcopasites* that I have examined. The two eyes of *S. gussakovskyi* are alike, and therefore probably not partially abraded. The labrum of the specimen is less elongated than that of any *Holcopasites* species now known (cf. Figs. 6, 9; also cf. Figs. 7, 9 of the very differently proportioned mesepisterna).

Interrelations of *Holcopasites* and *Schmiedeknechtia*

All who have studied at first hand (or considered the published) structural similarities and dissimilarities of the Palearctic *Schmiedeknechtia* (hereafter *Schm*) and Nearctic *Holcopasites* (*Holc*) agree, as I do: they are closely similar entities (Popov 1934, Grütte 1935, Linsley and Michener 1939, Mavromoustakis 1959, 1963, Hurd and Linsley 1972, Warncke 1982). However, not all agree as to their proper taxonomic status.

Popov doubted their separateness at a generic level. He pointed specifically to an absence of "sufficiently distinct differences" in forewing venation, and to the "complete similarity" of the male aedeagus ("genitalia") and male sterna-7 and -8 which he regarded to be of overriding significance. The dissimilarities he noted for the separation of *Holc* and *Schm* are weak by comparison. Of them, only the antennal differences hold for all *Holc*: 12-segmented antennae in both sexes of *Holc*, longer and 13-segmented antennae in the males of *Schm*. Nevertheless, Popov failed to propose their synonymy; Warncke, however, did so.

Because 12 ♀/12 ♂ antennal segmentation occurs in but one of the otherwise plesiomorphic species of *Biastes* (~9 species) and similarly in but one species of *his Pasites* (with more than 50 species),[3] Warncke (1982) claimed that the difference in male antennal segmentation is of specific value only. For that reason, he regarded the plesio-/apomorphic antennal difference between *Schm* and *Holc* males of no generic significance. In his view, therefore, *Holcopasites* Ashmead 1899 is a junior synonym of *Schmiedeknechtia* Friese 1896, and *Schmiedeknechtia* in turn is declared a subgenus of *Ammobatoides* Radoszkowski 1817.

Do cladistic and biogeographic studies shed light on the status of the two entities, *Schmiedeknechtia and Holcopasites*? Alexander's (1990) consensus tree (Fig. 4) and tables of character states (appendices 3, 5, largely drawn from the writings of others[4]) convincingly point to the monophyly of *Holc* and *Schm*, as expected. Michener's (1979) biogeographic study suggests that the Nomadinae *s. lat.* had their origins in the New World from anthophorine stocks which later spread from North America to the Old World; such spread and crossing of the North Atlantic may have occurred as recently as early Eocene, a time of suitable climate and a dry land connection (v. Smith et al. 1981, McKenna 1983).

At least two lines separated from the holcopasitine stem: that giving *Holc*, now found in Austral regions of North America, and that of *Schm*, now ranging the Mediterranean subregion of the Palearctic (see map 1, Bartholomew et al. 1911). Those two lines have been disjunct at least from the onset of Oligocene times, ±37 million years ago, and members of each now parasitize species of different panurgine genera. Significantly, *all* three described species of *Schm* retain the plesiomorphic antennal segmentation (12 ♀/13 ♂), and *all* 17 species of *Holc* display the distinguishing antennal apomorphism (12 ♀/12 ♂). Warncke cannot be supported in his claim that that distinction is

[3] Warncke, op. cit., regards the Nearctic *Neopasites* as a junior synonym of the Palearctic *Biastes*. He also lumps six genera, including *Ammobates*, with *Pasites*. The tribal name Pasitini thus replaces Ammobatini in his classification. Numbers of relevant species in Warncke's generic assignments are estimated from Alexander (1990; table 2).

[4] There are at least four relevant errors in scored character states, and one misstatement; they do not cause difficulty with the consensus cladogram as portrayed. They are: *Biastes* includes both states 8_0 and 8_1 (Friese 1895, Warncke 1982); species of both *Schm* (see Mavromoustakis 1959, figs. 2–4) and *Holc* have male pygidial conformations in addition to that of 29_1; character 1 would be better defined in terms of whether the labral apex surpasses the closed mandibles, for none of the 13 species of *Holc* examined by me has a ratio of labral length to width ≥ 1.5; a male of *S. gussakovskyi* Popov, with the labrum fully exposed, has a length : width ratio of 1.0.

only of a specific nature for *Holc* and *Schm* today. It may have been so for the immediate ancestor of today's *Holc,* but assuredly no longer applies to the numerous descendent species which are products of an early cladogenic event. Surely that is the likely history of most apomorphisms which separate supraspecific taxa today.

No thoroughgoing comparative study of both nominal genera and all of the species of the Holcopasitini has been made to date. That study should include mouthparts, aedeagus and male genital segments, details of at least female sternum-6, and of immature stages if available. The burden of proof of synonymy of *Holcopasites* with *Schmiedeknechtia* seems properly to lie with those who would accept Warncke's (1982) decision.

Acknowledgments

I am grateful to Drs. E. Gorton Linsley, University of California, Berkeley, Charles D. Michener, University of Kansas, and Jerome G. Rozen, Jr., American Museum of Natural History, all of whom were provided with a male and female paratype of *Holcopasites ruthae,* for kindly reviewing the descriptions of the two new bees and my commentary upon them. Any errors remaining are my own.

Dr. Michener also provided me with a partial translation of Popov (1935), as well as loan of a male specimen of *Schmiedeknechtia gussakovskyi*; he could not have been more helpful. Dr. Ronald J. McGinley and Ms. Maureen Mello of the U.S. National Museum of Natural History made loans of specimens of five species of *Holcopasites.* Through the efforts of Saul Frommer (of the University of California, Riverside), the long missing collection of Timberlake's small nomadines was found and kindly placed at my disposal.

My warm thanks to the above and to John Chemsak, University of California, Berkeley, S. P. Cover, Museum of Comparative Zoology at Harvard, Andrew Sanders, University of California, Riverside, Botanical Garden, and Drs. Terry L. Griswold, U.S.D.A. Bee Biology and Systematics Laboratory at Logan, Utah, John LaSalle, C.A.B. International Institute of Entomology, Alvin F. Shinn, William Paterson College of New Jersey, and W. P. Stephens, Oregon State University, all of whom responded most helpfully to my requests for information.

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